Mem. Qd Mus. **18**(2) 157–64 [1978]

THE NATURE OF THE MOLAR-PREMOLAR BOUNDARY IN MARSUPIALS AND A REINTERPRETATION OF THE HOMOLOGY OF MARSUPIAL CHEEKTEETH

MICHAEL ARCHER
Queensland Museum

ABSTRACT

Recent studies of dental ontogeny and abnormalities in marsupials indicate that all systems of homology in current use are incorrect, in part because all are based on the evidently erroneous assumption that true post-canine tooth replacement occurs in marsupials.

A new terminology is presented which accounts for all morphological and ontogenetic data, including the apparent phenomenon of Zahnreihen in dasyurid dentitions. This concept is three premolars, P1–3, a deciduous first molar, M1, and four permanent molars M2–5. Marsupials are therefore regarded to have three premolars, five molars, and no true post-canine milk-teeth. Some marsupials and in particular some kangaroos have six or more molars but these have been additions to the posterior end of the molar series.

Owen (1840–5) introduced stability into dental terminology by defining premolars as those post-canine teeth anterior to, and including, the posterior-most tooth having a milk-tooth predecessor. Teeth posterior to this tooth were regarded as molars. Application of this concept to marsupials has been complicated by interpretation of ontogenetic evidence. Spurious swellings along the free edge of the dental lamina have sometimes been interpreted as incipient or vestigial tooth buds representing replacement teeth. These interpretations have often given rise to conflicting terminologies. More recently, ontogenetic studies (Berkovitz 1967a, Archer 1974) of structurally primitive marsupials have confirmed earlier research (e.g. Woodward 1893) suggesting that the replaced tooth, M1 (in the terminology used here, but dP4 in the terminology of Thomas 1888, Table 1) does not give rise to the tooth germ of the replacing tooth P3 as it should if it were a member of the P3 premolar tooth family. For this reason, it has been suggested (Archer 1974) that cheekteeth in dasyurid marsupials cannot be classified as premolars or molars using Owen's (1840–5) system, and that recognition of Zahnreihen (in the sense of Woerdman 1921) or tooth developmental sequences may provide a means for classification of marsupial teeth independent of the phenomenon of tooth replacement.

Examination of marsupial groups reveals many differences in dental morphology and patterns of tooth development. An attempt has been made here to clarify these patterns using tooth morphology and ontogeny and to interpret homology of cheekteeth.

Terminology of crown morphology is set out elsewhere (Archer 1975a, 1976b, 1976c) or, if different from this, follows Bensley (1903) and Stirton (1967). Terminology of post-canine cheektooth number follows in part Owen (1845) and Stirton (1955), and not Thomas (1888) whose system I have previously used. It differs from Stirton's nomenclature in that the deciduous post-canine cheektooth is called M1. The nomenclature used here is therefore P1–3, M1, and M2–5. Owen (1845) and Stirton (1955) regard that there are three adult premolars, P1, P2, and P3, and the deciduous tooth in the cheektooth row of polyprotodonts is called dP3 (see Table 1). This deciduous tooth is called M1 in this paper. Marsupial names are used in the sense of Ride (1970), Laurie and Hill (1954), Clemens (1966), and Kirsch (1968). Specimen number prefixes used are as follows: J, JM, or F, Queensland Museum.

TABLE 1: POSTCANINE CHEEKTOOTH NOMENCLATURE USED IN THIS WORK, AND THAT OF THOMAS (1888) USED IN PREVIOUS WORKS, WITH DIAGRAMS OF UPPER AND LOWER CHEEKTEETH OF SEVEN REPRESENTATIVE MARSUPIAL GROUPS.

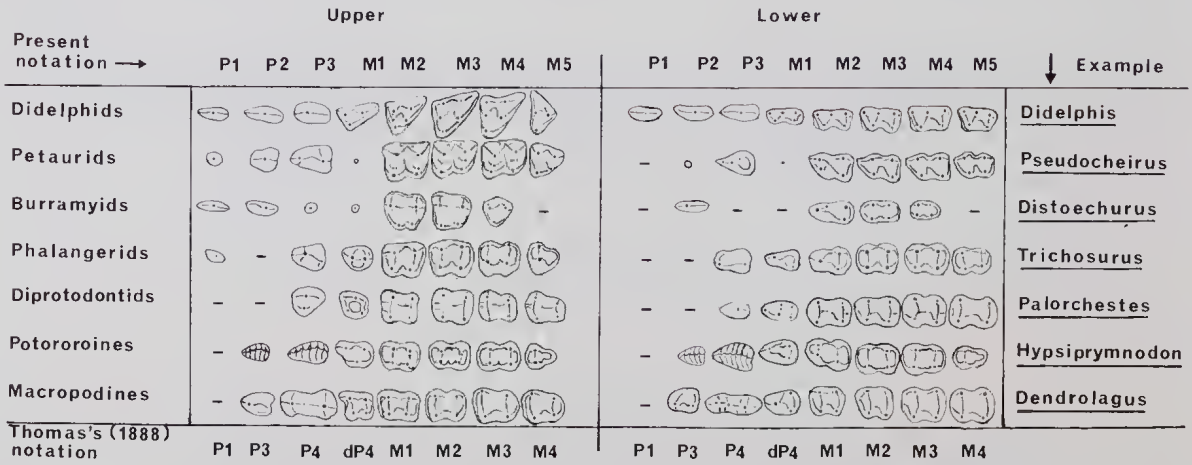

TABLE 2: NOTATIONAL SYSTEMS FOR MARSUPIAL POST-CANINE CHEECKTEETH INFERRED FROM ONTOGENETIC STUDIES AND COMPARED WITH THOMAS (1888).

Author									Group examined
Thomas (1888)	P1	P3	P4	dP4	M1	M2	M3	M4	Marsupials
Berkovitz (1967)	P1	P2	P3	M1	M2	M3	M4	M5	Didelphids
Archer (1974)	P1	P2	P3	M1	M2	M3	M4	M5	Dasyurids
Wilson and Hill (1897)	P1	P2	P3	dP3	M1	M2	M3	M4	Peramelids
Berkovitz (1968)	P1*	P2	P3	M1	M2	M3	M4	M5	Phalangerids
Bolk (1929)	P1	P2	P3	M1	M2	M3	M4	M5	Phalangerids
Berkovitz (1966)	P1	P2*	P3	M1	M2	M3	M4	M5	Macropodids

*Initiate but do not form part of functional dentition.

ONTOGENY

Recent ontogenetic work (Table 2) has revealed that in the dasyurid *Antechinus flavipes* there appear to be eight post-canine tooth families each of which has only one generation (Archer 1974). They develop in a time sequence as two distinct series: P1, P2, P3; and M1, M2, M3, M4, M5 (P1, P3 P4, dP4, M1–4 of Archer 1974). These series or Zahreihen are also morphologically uniform such that the teeth of the first are premolariform and those of the second molariform. Berkovitz (1967a), similarly demonstrates that in at least one didelphid, the tooth regarded here as P3 develops from the dental lamina between P2 and M1 and is therefore not a replacement tooth for M1.

Berkovitz (1966) also shows that a similar situation exists in at least one macropodid. It may also occur in one phalangerid (Bolk 1929, Berkovitz 1968) but the evidence is not clear. Kirkpatrick (1969) demonstrates a developmental relationship between the teeth regarded here as M1, M2, M3, M4 and M5 in several macropodids, and an apparently close relationship between P2 and P3. He suggests M2–4 are successional teeth in the M1 family.

These studies demonstrate M1 to be part of a molariform cheektooth series and evidently unrelated to P3 in at least three marsupial families, including didelphids and dasyurids which are structurally ancestral to other marsupial groups.

Morphology

Bensley's (1903) important examination of marsupial cheektooth morphology serves as a basis for further comparisons, and in particular, a closer examination here of the P2, M1, P3, M2 region. Ride (1961) realizes the importance of this region in determining cusp homology in macropodids and it also seems to be the important region in interpreting homology in macropodid and phalangerid cheektecth.

To avoid lengthy descriptions, the juvenile and adult P1–M5 region of the dentition of representative marsupials are shown in outline form in Table 1 and attention is given below only to particular aspects of these dentitions.

Individual Cheekteeth (P2, P3, M1, M2)

P2: Because there has been no satisfactory demonstration of more than three premolars in marsupials, it is possible that P2, in all marsupials with three premolars in the adult dentition, are homologous teeth. In dasyurids with less than three, it is always P3 which has been lost (Archer 1976a). In phalangeroids with less than three upper premolars (e.g. phalangerids, macropodids, and diprotodontids) homology of the anterior premolar is uncertain. Berkovitz (1966) demonstrates that in at least one macropodid the anterior adult premolar is the second of three teeth to develop on the dental lamina posterior to the canine. The first tooth develops but later disappears. However, Berkovitz (1968) demonstrates that in at least one phalangerid, the anterior adult premolar is the first of three to develop on the dental lamina posterior to the canine. The second tooth develops but does not persist. Homology of lower antemolar teeth in phalangeroids is extremely uncertain, most early ontogenetic studies having misinterpreted true milk incisor teeth for vestigial tooth families (e.g. Woodward 1893).

Kirkpatrick (1969) has examined tooth development in some macropodids and concludes that P2 is a milk-tooth which is later replaced by P3, a second generation tooth in the P2 tooth family. This view is not supported by other ontogenetic studies on macropodids such as those of Berkovitz (1966) where P3 develops from the dental lamina between P2 and M1. The interpreted differences may result from post-initiation degenerative changes in the dental lamina or by shifts in relative position due to migration of tooth buds or development of the free edge of the dental lamina. Before the actual homologies of P2 and P3 in macropodids can be determined, ontogenetic studies should be carried out on potoroine macropodids where P2 and P3 are large and the possible masking effects of tooth migration are reduced.

Morphology of P2 in all marsupials in which it has not been lost is either premolariform or caniniform. In some potoroine macropodids, and some caenolestoids, it is a plagiaulacoid sectorial tooth. In *Phalanger* it is caniniform. In no group is it molariform.

P3: Ontogenetic evidence in didelphids, dasyurids, phalangerids, and macropodids suggests P3 is the posterior member of a premolariform Zahnreihe. It develops from the dental lamina anterior to M1 and posterior to P2. Abnormal teeth interpretable (Archer 1975) as P^4 (P5 of Archer 1975) in some macropodids, and inferred to develop posterior to P^3 on the dental lamina, are also premolariform.

Morphologically, P3 is never molariform although the posterior end may become secondarily molarized in quadritubercular or lophondont forms such as phascolarctids, macropodids, and diprotodontids. In potoroine macropodids, caenolestoids, some burramyids and incipiently in some phalangerids, P3 tends towards or is a well-developed plagiaulacoid sectorial tooth. Broom (1896) suggests the sectorial premolars of *Burramys* (a burramyid) and *Hypsiprymnodon* (a macropodid) are completely unlike those of phalangerids because the serrations are on opposite ends of the tooth. This observation seems of little import in view of the fact that in other macropodids (e.g. some *Bettongia* and *Potorous*) the serrations occur in the middle of the tooth without actually reaching the anterior end. In some of these forms (as noted by Ride 1956) the smooth anterior portion of the sectorial premolar is longer than the smooth posterior portion, the opposite of the condition found in *Hypsiprymnodon*. In caenolestoids a comparable range of morphology suggests position of serrations is not significant in diagnosing groups above the generic level.

M1: Ontogenetic studies (Archer 1974) of dasyurids suggest that M1 (called dP4 by Archer 1974) is the most anterior member of a posterior molariform Zahnreihe which includes M1–M5. Kirkpatrick (1969) has similarly suggested that M1 and M2–5 (his dP4 and M1–4) in macropodids develop as related series of teeth, although he does not interpret the relationship as a Zahnreihe. Sequence of tooth development in the macropodid *Setonix* noted by Berkovitz (1966) is similar to that in dasyurids.

From a survey of M1 morphology (to be published), it is also apparent that these teeth, in all marsupials in which they are not reduced to vestiges, although rarely premolariform, are frequently molariform. Therefore morphology and ontogeny is used here to conclude that the marsupial deciduous cheektooth is actually the first molar, i.e. M1, there being no true post-canine tooth replacement. In contrast is the more traditional view of Owen (1840–5) and most later workers who believe that this tooth is a true milk-premolar that secondarily has become molariform. Indirect evidence for Owen's view is the well-known fact (e.g. Butler 1952) that in many eutherian groups dP3 has undergone molarization to either increase the number of functional molariform teeth in juveniles, or to shift anteriorly the molariform–premolariform boundary. I do not think this is the case in marsupials for four reasons. First, the oldest known (Cretaceous) marsupials have an extremely well-developed molariform M1 (e.g. Clemens 1966) which might not be the case if molarization of a deciduous premolar was a secondary development unless secondary molarization occurred extremely early in primitive marsupials. Secondly, except for didelphids, macropodids, and some phalangerids, the marsupial M1 is almost invariably too small to be functional and it seems improbable that it would secondarily evolve molariform characters when it never really has a chance to function as a molar. In at least some modern didelphids (Archer 1976) M1 is comparable in complexity to the same tooth in Cretaceous didelphids, thereby providing no evidence for secondary molarization. In macropodids it is probable that M1 has become secondarily molarized, but there is no evidence that this process of molarization in macropodids started with a premolariform M1. Third, there appears to be a repetitive basic crown pattern in M1 in distantly related groups including some dasyurids, phalangerids, and diprotodontids which suggests the possibility that an 'archetypal' molariform pattern may persist rather than develop polyphyetically in teeth which are free from heavy selective pressure. Fourth, recent ontogenetic evidence indicates M1 is part of the molariform tooth series and not a predecessor to P3.

The improbability of a tooth family relationship between M1 and P3 is further indicated by the various ways in which tooth reduction occurs in this position. In many dasyurids, thylacinids, peramelids, and diprotodonts such as phascolaretids and Petaurids (Archer 1975), M1 is tiny or absent while P3 is large. Yet in other diprotodonts such as some phalangerids, M1 is only slightly smaller than P3, and in macropodine macropodids, M1 is markedly larger than the small P3. Ziegler (1971) has suggested that in mammals in general reduction of premolar number occurs first by loss of the permanent tooth and only later by loss of the deciduous tooth. For this reason, the inconsistent pattern of tooth reduction in marsupials would suggest there is no true milk-tooth in the postcanine cheektooth row.

Morphology of M_1 in potoroine macropodids is similar to that of M_2 in many non-macropodid diprotodonts such as *Phalanger* and *Trichosurus*. Broad aspects of this similarity have been noted by Bensley (1903) and Ride (1961) both of whom regard it as occurring in non-homologous teeth in the two groups. Ride (1961) also regards the cusps involved in the compressed trigonids of these similar teeth to differ. The principal cusp on the trigonid of M_2 in phalangerids (see below) is regarded here (and by Ride 1961) to be the protoconid. However, Ride (1961) regards the principal cusp of M_1 in *Hysiprymnodon* to be the metaconid, a conclusion based on his interpretation of a small cupsule on the posterior slope of the main cusp as the protoconid, and of the apparent topographic serial homology of this cuspule with a cuspule on M_2 in the position of a protoconid. If Ride is right, the apparent similarity between M_2 of phalangerids and M_1 of macropodids is the result of convergence. It is suggested below that the anterobuccal cusp on M_2 of petaurids and phascolaretids is, as Bensley (1903) concludes, a neomorph or protostylid, the protoconid having shifted lingually. Phascolarctids are also regarded by some authors (Winge 1941, Archer 1976) as structurally ancestral to other diprotodonts. Therefore it is possible that the anterobuccal cusp in M_2 of *Hypsiprymnodon* (and other macropodids) is the homologue of the phascolaretid protostylid, and not the protoconid. The tiny cusp observed by Ride (1961) on M_1 of *Hypsiprymnodon* may be the serial homologue of this protostylid, the high cusp on that tooth again being the protoconid. The compressed condition of the trigonid of M_2, and relatively slight development of the anterobuccal cusp in *Hysiprymnodon* might then be regarded as structurally ancestral characters. Pressure to molarize M_2 and M_1 has resulted in enlargement of this cusp in M_2 of all and M_1 of most other macropodids.

Further support for the possibility that the protoconid is anterolingual on trigonids of M_1 in macropodids is provided by Berkovitz (1967b). In

an ontogenetic study of crown development in *Setonix* he shows that although the anterobuccal cusp of M_2, interpreted by him to be the protoconid, develops first, the anterolingual cusp of M_1 develops first. Accepting Ride's (1961) interpretation of this cusp as the metaconid, Berkovitz concludes that ontogeny of M_1 in *Setonix* is not therefore recapitulating phylogeny because the protoconid is generally regarded as the original trigonid cusp. Although the principal of ontogeny recapitulating phylogeny in marsupial tooth cusps has been questioned elsewhere (Archer 1975), in the present case the early development of the lingual cusp is more consistant with its interpretation as a protoconid than a metaconid.

Although these points are made in order to indicate that the cusps of molariform teeth with compressed trigonids in different groups of diprotodonts may be homologous, it does not necessarily indicate that the teeth themselves are homologous.

M2: Previous confusion in interpretation of M_2 cusp homology has resulted from examination of worn molars. Ride (1961) points out that Bensley (1903) must have had only worn specimens of *Hypsiprymnodon* resulting in his failure to correctly interpret the number of cusps on M_2. Ride (1961) and Bensley (1903), however, seem to have had only worn specimens of *Phascolarctos*. Because I regard the morphology of *Phascolarctos* to be basic to at least an understanding of other diprotodont groups (Archer 1976), it is of interest here to briefly describe the morphology of its M_2 (e.g. J13278). The tooth have five principal cusps forming apices of crests. The talonid has a buccal hypoconid and a lingual entoconid. The cristid obliqua crosses from the hypoconid to the tip of the tallest trigonid cusp, the protoconid. This cusp is just lingual to a medial position on the trigonid. The protoconid is connected by a posterolingual crest to the metaconid. A paracristid extends anteriorly from the protoconid to the anterior end of the tooth, the topographic position of a missing paraconid. Buccal to the cristid obliqua, protoconid, and paracristid, a well-developed accessory crest, with a neomorphic cusp at its apex, extends from the anterior base of the hypoconid to the anterior tip of the tooth. Bensley (1903) suggests that this anterobuccal cusp is a new development and not homologous with the protocone of succeeding molars. I entirely agree, and do not regard this interpretation as a violation of the concept of serial homology, which leads Ride (1961) to suggest that the only cusp he observes on the anterolingual end of M_2 is the metaconid and the anterobuccal cusp is the protoconid. Ride also regards the anterobuccal cusp in *Pseudocheirus*, which is smaller, to be the protocone. Here again, details of unworn molars as well as a comparison of the M_2 of most species of *Pseudocheirus*, make it reasonably clear that the anterobuccal cusp in *Pseudocherus* is the homologue of the protostylid in *Phascolarctos* and not the protoconid. In *Pseudocheirus*, as in *Phascolarctos*, the protoconid is the high anterolingual cusp, with a posterolingual, variably cuspid crest representing the metaconid.

The M_2 of *Hypsiprymnodon* differs from that tooth in phalangerids, phascolarctids and petaurids, but is adequately illustrated and described by Ride (1961). In other macropodids, morphology of M_2 is similar to *Hypsiprymnodon* but lacks the slight lateral compression of the trigonid.

It is clear that in all macropodids the anterobuccal cusp on M_{3-5} is the protoconid, as concluded by Ride (1961). The alternative view, proposed by Bensley (1903), that this cusp is the homologue of the phascolarctid protostylid of M_2, is not acceptable. However, Ride's conclusion that there is no evidence for suggesting M_2 in macropodids was ever other than quadritubercular, is doubtful because the anterobuccal cusp on M_2 may not be the protoconid.

M_2 of all diprotodonts except most macropodids and all diprotodontids has a laterally compressed trigonid. As a result of this compression, the paracristid assumes a longitudinal orientation by lingual displacement of the protoconid. In almost all diprotodonts, the degree of compression correlates with the degree of sectorial development of P_3. A culmination of this trend may be seen in thylacoleonids where the trigonid of M_2 is a massive, longitudinal shearing crest. The opposite extreme is found in some diprotodontids and macropodids where P_3 is frequently almost round and tubercular and the trigonid of M_2 lacks any compression. The fact that in *Phascolarctos* attempts to molarize the M_2 trigonid result in development of a new cusp, rather than a buccal shift of the protoconid, indicate the stability of the laterally compressed trigonid in diprotodonts. In polydolopid (and possible abderitine) caenolestoids, the compressed trigonid of M_2 is not clearly formed in the same way as it is in diprotodonts. The analogue of the short longitudinal paracristid may be a new development unrelated to the actual positions of the protoconid and paraconid.

Concepts Of Cheektooth Homology In Polyprotodont Marsupials

As indicated above from ontogenetic and morphologic data, dasyurids and didelphids have eight posteanine cheekteeth which are most appropriately interpreted as P1–3, M1 and M2–5 (where M1 is the nomeclatural equivalent of the dP3 of Stirton 1955). There is nothing about perameloids to suspect they differ from this basic polyprotodont pattern. Wilson and Hill (1897) have shown that P3 appears to develop from dental lamina lingual to the developing M1 but their data do not show that it could not be comparable with the dasyurid situation described by Archer (1974) where P3 appears to develop from the dental lamina between P2 and M1, and only secondarily comes to lie lingual to M1 as the tooth buds grow and crowd the developing tooth row as a whole.

Stirton (1955) employs the tooth nomenclature P1–3, dP3, M1–4. This nomenclature is also used by almost all modern Americans (e.g. Woodburne, Tedford, Clemens, Marcus, Lillegraven, Campbell) as well as by some Australian zoologists (e.g. Bartholomai, Marshall, Plane) who do not follow Thomas (1888). Although based on the concept of tooth replacement, it purports to avoid implying that a particular premolar tooth family has been lost in marsupials. As Mahoney and Ride (1975) point out, no system of numbering can avoid implying homology, and it could be concluded from Stirton's terminology that marsupials have lost the original P4 of their common ancestor with placental mammals, even though Stirton did not intend to imply this concept.

The common alternative is the system of Thomas (1888) which is P1, P3-4, dP4, M1–4. It is used by many zoologists in Australia and England (e.g. Ride, Archer in previous works, Mahoney, Berkovitz, Merrilees, etc.) and some American zoologists (e.g. Tate). Because of its wide use among Australian zoologists, I adopted it in earlier works. However, it is based on two apparent misconceptions: that the homologue of the placental P2 is missing from the marsupial tooth row (the lack of acceptable evidence for this is reviewed by Archer 1974, 1975); and that M1 (dP3 of Stirton) is a true milk-tooth.

Ziegler (1971) also accepts the apparently erroneous concept of cheektooth replacement in marsupials, but differs from Thomas (1888) in regarding marsupials to have lost P1, accordingly designating the functional adult premolars P2, P3 and P4. Lundelius and Turnbull (e.g. 1973) also use this system but regard homology of P2 to be doubtful.

Reasons for not accepting any current concept of loss of a particular premolar family in structurally primitive marsupials are given elsewhere (Archer 1975). Although it does seem probable that ancestral marsupials lost a premolar family which they must have shared in their common ancestor with placentals, there is as yet no conclusive morphological, ontogenetic, or palaeontological evidence for this loss.

Concepts Of Cheektooth Homology in Diprotodont Marsupials

Reports of the significance of residual lingual and spurious buccal traces of dental lamina in diprotodonts are not considered here. They are adequately reviewed by Berkovitz (1966) who concludes that most lingual downgrowths are merely residual free ends of dental lamina and do not represent vestigial replacement teeth.

In all diprotodont marsupials there are fewer teeth in the total dentition than in any polyprotodont. Most of the reductions in number involve incisors, canines and premolariform teeth. Petaurids have the highest diprotodont tooth number and, at least in their upper postcanine cheekteeth, the number is identical with polyprotodont marsupials. Further, they show the same manner of apparent tooth replaeement as polyprotodonts. They differ from most polyprotodonts in that the M^1 is very tiny (Archer 1975). In some other diprotodont families, such as the diprotodontids and phalangerids, M^1 is much larger and functional. Therefore in at least these diprotodont groups, morphologieal as well as the limited ontogenetie data support the cheektooth homology of P1–3, M1, M2–5.

Macropodid diprotodonts are unique among marsupials in that P3 during eruption replaces the teeth regarded here as P2 as well as M1. This raises the possibility that the macropodid M1 is not homologous with M1 of other marsupials, a possibility however which is negated by the ontogenetic evidenee that in macropodids, as in all marsupials, M1 is the first molar. Similarly, comparisons of the phalangerid M_2 with the maeropodid M_1 reveal at least a basieally similar trigonid construction and could be regarded as evidence that the teeth are homologous. However, if these two teeth were regarded as homologues, it would be necessary to ignore the ontogenetic data whieh indicates that the macropodid M_1 is a first molar and the phalangerid M_2 is a second molar. The posterior deciduous eheekteeth in the two groups, i.e. M1, also show similarities in trigonid construction and if these teeth are regarded as homologues, there is no conflict with ontogenetic data.

In summary, there is no evidence for suggesting that the homology of the cheekteeth in diprotodont marsupials differs from that of polyprotodont marsupials. Even kangaroos, with their unique number of deciduous cheekteeth, lack any true postcanine milkteeth and are thus essentially similar to other marsupials.

CAENOLESTOIDS

There is no evidence for apparent tooth replacement in living caenolestids in over 150 specimens of *Caenoloestes*, *Orolestes* and *Rhyncholestes* examined by the author in museum collections. Similarly, there does not appear to be any evidence for tooth replacement in the great variety of known fossil caenolestoids, including those forms with large plagiaulacoid premolars. If tooth replacement of the sort which occurs in other marsupial orders does occur in caenolestoids, it must occur very early in ontogenetic development. Assuming this is the case, the maximum caenolestoid postcanine cheektooth dentition would be P1–3, M1 (not yet observed), M2–5. If tooth replacement does not occur, then it is possible that caenolestoids represent a unique order of marsupials all members of which have no more than seven postcanine cheekteeth.

DISCUSSION

All morphologic and ontogenetic evidence in polyprotodont and diprotodont marsupials leads to the conclusion that there are three premolar tooth families and five molar tooth families the first of which is deciduous.

This conclusion has brought me to an impasse. If these data are acknowledged but not used, there is a possibility that in using an alternative and less probable system, comparisons of particular teeth within the various marsupial groups and between marsupials and placentals may be meaningless.

For this reason, although I have previously used the system of Thomas (1888), I intend to use the nomenclature P1–3, M1, and M2–5 until it is shown to be wrong or less probable than an alternative system.

ACKNOWLEDGEMENTS

Dr A. Bartholomai and Mr B. Campbell (Queensland Museum) read and constructively criticised a draft of this work. Ms R. Owen and Mrs C. Farlow (Queensland Museum) typed drafts of the manuscript.

Early concepts from which this work has developed were discussed with Dr W. D. L. Ride (then Director of the Western Australian Museum) and the present work owes much to his stimulation.

LITERATURE CITED

ARCHER, M., 1974. The development of the cheek-teeth in *Antechinus flavipes* (Marsupialia, Dasyuridae). *J. Roy. Soc. West. Aust.* **57:** 54–63.

1975a. The development of premolar and molar crowns of *Antechinus flavipes* (Marsupialia, Dasyuridae) and the significance of cusp ontogeny in mammalian teeth. *J. Roy. Soc. West. Aust.* **57:** 118–25.

1975b. *Ningaui*, a new genus of tiny dasyurids (Marsupialia) and two new species, *N. timealeyi* and *N. ridei*, from arid Western Australia. *Mem. Qd Mus.* **17:** 237–49.

1975c. Abnormal dental development and its significance in dasyurids and other marsupials. *Mem. Qd Mus.* **17:** 251–65.

1976a. The dasyurid dentition and its relationships to that of didelphids, thylacinids, borhyaenids (Marsupicanivora) and peramelids (Peramelina, Marsupialia). *Aust. J. Zool. Suppl. Series No.* **39:** 1–34.

1976b. The basicranial region of marsuipicanivores (Marsupialia), interrelationships of carnivorous marsupials, and affinities of the insectivorious marsupial peramelids. *J. Linn. Soc. Lond (Zool.)* **59:** 217–322.

1976c. Phascolarctid origins and the potential of the selenodont molar in the evolution of diprotodont marsupials. *Mem. Qd Mus.* **17:** 367–371.

BENSLEY, B. A., 1903. On the evolution of the Australian Marsupialia: with remarks on the relationships of the marsupials in general. *Trans. Linn. Soc. Lond. (Zool.) (2)* **9:** 83–214.

BERKOVITZ, B. K. B., 1966. The homology of the premolar teeth in *Setonix brachyurus* (Macropodidae: Marsupialia). *Archs oral Biol.* **11:** 1371–84.

1967a. The dentition of a 25-Day pouch-young specimen of *Didelphis virginiana* (Didelphidae: Marsupialia). *Arch oral Biol.* **12:** 1211–2.

1967b. The order of cusp development on the molar teeth of *Setonix brachyurus* (Macropodidae: Marsupialia). *J. Roy. Soc. West. Aust.* **50:** 41–8.

1968. Some stages in the early development of the post-incisor dentition of *Trichosurus vulpecula* (Phalangeroidea: Marsupialia). *J. Zool. Lond.* **154:** 403–14.

BOLK, L., 1929. Die Gebissentwicklung von *Trichosurus*. *Gegensbaurs morph. Jb.* **62:** 58–178.

BROOM, R., 1896. On a small fossil marsupial with large grooved premolars. *Proc. Linn. Soc. N.S.W.* **10:** 563.

BUTLER, P. M., 1952. Molarization of the premolars in the Perissodactyla. *Proc. Zool. Soc. Lond.* **121:** 819–43.

CLEMENS, W. A., 1966. Fossil mammals of the type Lance Formation, Wyoming, Part 2. Marsupialia. *Bull. Dep. Geol. Univ. Calif.* **62:** 1–122.

KIRKPATRICK, T. H., 1969. The dentition of the marsupial family Macropodidae with particular reference to tooth development in the grey kangaroo *Macropus giganteus* Shaw. PhD thesis, University of Queensland.

KIRSCH, J. A. W., 1968. Prodromus of the comparative serology of Marsupialia. *Nature, Lond.* **217:** 418–20.

LAURIE, E. M. O., HILL, J. E., 1954. 'List of land mammals of New Guinea, Celebes and adjacent islands 1758–1952', 175pp (Tonbridge Printers Ltd: Tonbridge).

MAHONEY, J. A., RIDE, W. D. L., 1975. Index to the genera and species of fossil Mammalia described from Australia and New Guinea between 1838 and 1968. *Spec. Publs. West. Aust. Mus.* **6:** 1–250.

OWEN, R., 1840–5. 'Odontography; or, a treatise on the comparative anatomy of the teeth; their physiological relations, mode of development, and microscopic structure, in the vertebrate animals', Vol. 1, lxxiv and 655 pp. (Hippolyte Baillière: London).

RIDE, W. D. L., 1956. The affinities of *Burramys parvus* Broom a fossil phalangeroid marsupial. *Proc. Zool. Soc. Lond.* **127:** 413–29.

1961. The cheek-teeth of *Hypsiprymnodon moschatus* Ramsay 1876 (Macropodidae: Marsupialia). *J. Roy. Soc. West. Aust.* **44:** 53–60.

1970. 'A guide to the native mammals of Australia', xiv and 249 pp. (Oxford Univ. Pr.: Melbourne).

STIRTON, R. A., 1955. Late Tertiary marsupials from South Australia. *Rec. S. Aust. Mus.* **11:** 247–68.

TATE, G. H. H., 1947. On the anatomy and classification of the Dasyuridae (Marsupialia). *Bull. Amer. Mus. Nat. Hist.* **88:** 97–156.

THOMAS, O., 1888. 'Catalogue of the Marsupialia and Monotremata in the collection of the British Museum (Natural History)', xiii and 401 pp. (British Museum (Natural History) : London).

TURNBULL, W. D., LUNDELIUS, E. L., 1973. The mammalian fauna of Madura Cave, Western Australia Part 1. *Fieldiana (Geology)* **31:** 1–35.

WINGE, H., 1941. 'The interrrelationships of the mammalian genera', Vol. 1, xii and 418 pp. (C. A. Reitzels Forlag : Kobenhavn).

WOODWARD, M. F., 1893. Contributions to the study of mammalian dentition. Part 1. On the development of the teeth of the Macropodidae. *Proc. Zool. Soc. Lond.* **1893:** 450–73.

ZIEGLER, A. C., 1971. A theory of the evolution of therian dental formulas and replacement patterns. *Q. Rev. Biol.* **46:** 226–49.